THE RELATION OF TEMPERATURE AND HUMIDITY TO INFECTION BY CERTAIN FUNGI

A THESIS

Presented to the Faculty of the Graduate School
of Cornell University for the Degree of
Doctor of Philosophy

By
JOHN IRVIN LAURITZEN

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J. I. LAURITZEN

INTRODUCTION

Very early in the history of plant pathology a fundamental relation between weather and plant diseases was recognized, not only by the pathologist but by the farmer. Even before anything was known about the nature of diseases, the weather was thought to have an intimate connection with their causes, and by many to be responsible for their production; and yet very little work has been done to analyze the exact manner in which weather conditions affect diseases or disease production, except in an observational way.

The effects of temperature, humidity, rainfall, and dew have not been isolated, except in a few cases, and then chiefly from observation or under partially controlled conditions. Never, so far as the author is aware, has the influence of temperature and humidity upon infection been studied separately where both have been under control.

The importance of taking cognizance of the one while studying the other in connection with any growth phenomenon will be emphasized from the following examples of the influence of temperature and humidity on the growth of bamboo. Shibata (28), working under field conditions in Japan, gives a table which indicates a close relation between the daily growth of bamboo and temperature (16°C. to 20°C.) and scarcely any relation to humidity. Lock (19), working at Peradeniya, on the other hand, found that the daily growth depends largely upon the water supply and the moisture content of the air, and has little relation to the temperature, which in his experiments fluctuated beween 19° and 26°C.

The difference in the temperature of the two places will account for the seeming discrepancy, as far as the temperature is concerned. At Peradeniya the temperature is apparently the optimum for the growth of bam-

[1] Also presented to the Faculty of the Graduate School of Cornell University, March, 1916, as major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy. The writer is indebted to Dr. Donald Reddick and Dr. V. B. Stewart under whose immediate direction the work was performed for valuable assistance and suggestions in connection with the investigation and in the preparation of the manuscript.

boo, and covers a range of several degrees, while in Japan it falls below the optimum, consequently the growth curve follows closely that of the temperature. A comparison of the humidity of the two regions, as far as a comparison is possible from the data that are available, reveals very little difference in the moisture content of the air. It is apparent that this humidity, which varies largely between 70 per cent and 90 per cent influences the amount of growth under the favorable temperature at Peradeniya. Its influence is evidently obscured by the unfavorable temperature in Japan. Whether the humidity can become so unfavorable as to obscure the effects of temperature is not known from the data at hand, but it is probable. One thing seems certain, however, that in studying either of these factors one cannot afford to ignore the one while the other is under observation; in fact, it would be preferable to hold one of these factors constant when observing the other.

In earlier work in pathology a clear distinction has not been drawn between the infection period and the period of incubation.[2] Such a differentiation is not always possible, and perhaps it is never possible to state definitely the exact point at which the infection period ends or the period of incubation begins. However, in most cases they can be separated sufficiently to study each apart from the other. Considerable work has been done to show the influence of temperature on the production and development of disease, but the two periods have been studied conjointly. Less work has been done upon the relation of humidity to this phenomenon but a sharper separation has been made between the infection and incubation periods.

Balls (4) conducted temperature-infection experiments with Rhizoctonia (*Corticium vagum* B. and C., var. *Solani* Burt) on cotton (*Gossypium spp.*) in which he found that infection took place and became evident in twenty-four hours at a temperature of 20°C. At 33°C. no infection occurred. Here the infection and incubation periods are crowded into such a short space of time and apparently so fused together that probably it would be difficult to separate them. The experiments were conducted by placing mycelium of the fungus in contact with seedlings placed upon several layers of moist filter paper in a petri dish, which in turn was placed in an infection chamber.

Gilman (11) performed some soil infection experiments with *Fusarium conglutinans* Wollenw. on cabbage (*Brassica oleracea* L.) which are of interest in this connection chiefly because he worked in a greenhouse in which the temperature was automatically controlled. He also conducted some

[2] Infection period as here used is the period during which the pathogen penetrates the host until it becomes established with the host. Incubation period is the period of development that follows until the symptoms of the disease become visible.

experiments in a glass infection chamber where the temperature was controlled by an electric thermo-regulator. The difficulty of studying infection apart from the incubation period is here apparent. It is not, however, so important in this instance that they should be studied separately, because the environmental factors are not so variable except in the case of temperature.

Tisdale (29) studied the infection of flax by *Fusarium Lini* Bolley. He found that the lower temperature limit for infection was about 15°C., and makes the statement that most of the infection occurs between 20° and 30°C. The temperature was controlled in one set of experiments by employing positions at different distances from a radiator in a green house, in another by means of a circulating water jacket about the plant containers. He also investigated the influence of temperature upon the growth of the fungus in culture media, and determined the limits to be 10° and 37°C. with an optimum temperature at 26° to 28°C.

Johnson (14), in working with *Thielavia basicola* Zopf. to test the range of parasitism on a large number of plants, controlled the moisture content of the soil and recorded the soil and air temperatures. The temperature of the air and soil depended upon greenhouse conditions.

Fromme (10) was unable to produce infection on oats (*Avena sativa* L.) by *Puccinia coronifera* Kleb. with a relative humidity of 75 per cent to 80 per cent and a temperature of 55° to 85° F. He conducted an experiment designed to determine what conditions of humidity were necessary for infection. He grew his plants in an open case made of window sashes where the humidity averaged 93 per cent with a variation of about 2 per cent to 3 per cent. Although he inoculated thoroughly, he obtained only slight infection. In an experiment where one pot was covered and another stood in an open box there was an average of 161.6 lesions per plant in the first case as compared with 10.4 or 6 per cent in the latter.

Some interesting results were obtained by Levin (17) in connection with an experiment planned to determine the time required for the infection of tomatoes (*Lcyoporsicum esculentum* Mill.) by *Septoria lycopersici* Speg. He sprayed ten plants with a water suspension of spores, placing 9 of them in a Wardian case, where a high humidity was maintained by means of a fine spray of water. A plant was taken out at intervals of 6, 12, 24, 36, 48, 60, and 72 hours and dried immediately by an electric fan and placed in an open window until infection became evident. After a lapse of five days all the plants, including the one left on the outside, showed characteristic lesions of the disease. This experiment was repeated in detail, except that the plants after inoculation were exposed to a current of air from an electric fan until the disease appeared. The results were similar to those secured in the previous experiment. Infection was also obtained by applying dry spores.

From the results of these experiments the author concludes that it is questionable whether a film of water over the plant surface for at least a number of hours is essential to infection.

The purpose of the present study is to determine the influence of temperature and humidity upon infection, and to find out whether a film of water covering the surface of the plant is essential for the fungus to become established upon the host.

APPARATUS

The apparatus consists of two double chambers with thermo-electric connections to furnish heat, and power to run fans. The outer chambers are 40 by 54 by 48 inches in size and are made of glass. The inner are 11 inches smaller in each dimension and so placed that there is an air space of 5 inches on all sides. They are constructed of wood except the lids, which are of glass and slope at an angle of 40° from the horizontal. The wood portion is coated on the inside with paraffin of a high melting point to prevent the absorption of water. Both inner and outer chambers are provided with heating coils and thermostats. In the latter case a relay was employed to prevent sticking of the thermostat, which was occasioned by the use of larger wire necessitated to produce the required heat for the outer chamber.

The evaporation surface for the control of the humidity was supplied by open pans containing either pure water or saturated salt solutions. The humidity was read directly from psychrometers upon which was directed a constant current of air from a fan.

FACTORS

In approaching any physiological problem one is confronted with certain difficulties. One of these is the isolation of the particular factor to be studied. The conditions affecting physiological processes are not only numerous, but complex, and sometimes so interrelated as to make their separation impossible.

The usual procedure is to hold all the other factors constant in order to get at the facts of the particular one to be observed. Having thus reduced the problems to simple terms, one might think he could proceed directly to the solution of his problem, but he soon finds that the procedure is not so simple. One should not only have the conditions constant, but they should be at their optimum, and such an accomplishment is by no means easy, if indeed possible, with our present knowledge of the nature of physiological processes, the factors affecting them, or methods of investigation.

In the present study an attempt has been made to keep the known and possible factors affecting infection constant as far as possible with the

means accessible. An attempt has been made to control, in part, conditions influencing the growth of the host plant, such as the fertility, physical properties, organic matter and water content of the soil, light, temperature, and humidity. The first four of these conditions are fairly easy to control; the latter three involve more difficulties. Temperature and humidity have been controlled as far as is possible under greenhouse conditions. Light is the most variable factor and no attempt has been made to control it. The greatest difference in light is between summer and winter. Whether this difference is sufficient to alter the susceptibility of the host plant to the attack of the fungus, or in any way influences the infecting ability of the fungus, is not known. No such influence has been noticed in the present experiments. It would seem that influences of light become less important when making comparison between the successive periods required for the growth of the plants while they attain sufficient size for inoculation purposes.

Temperature and humidity may affect each plant differently, which of course is true of the other factors. The exact range of temperature and humidity favorable for the growth of the plants employed in these experiments has not been determined. A variation in the range with the plant is, however, generally recognized. It would have been desirable to have grown these plants under optimum conditions, but these conditions were not available, besides the optimum for each of these plants is not known. These same conditions also come into operation during the incubation period.

Light as it exists under greenhouse conditions is not known to be a factor. Since light under natural conditions is not usually regarded as the limiting factor in photosynthesis, upon which host and parasite alike largely depend for their organic nutrition, it would seem that the reduction in food due to the reduction in light under greenhouse conditions would not be sufficient to alter the number of infections more than slightly, if at all.

It would seem reasonable to assume that temperature and humidity during the incubation period do not influence the total number of infections if sufficient time is allowed for the viable spores to establish a relation with the host. It is possible that the border-line temperatures and humidities might cause a variation in the susceptibility of the host to the parasite. There is some evidence to support this position in the case of temperature.

Ravn (25), in studying the influence of temperature upon the infection of barley by Helminthosporium, found that the incubation period was forty-eight hours in a warm greenhouse as compared with seventy-two hours in a cold house. The total amount of infection was slightly in favor

of the cold house. Fifteen out of 16 plants were infected in the cold house, while 12 out of 15 in the warm house were infected. He concludes from this experiment that temperature does not alter the total amount of infection.

Fromme (10) obtained similar results with *Puccinia coronifera* on oats. Plants inoculated and grown at a temperature ranging from 20° to 30°C. showed evidence of infection on the fourth day, while plants inoculated at the same time and grown in a greenhouse at a temperature varying-between 14.5° and 21°C. showed indications of the disease only after seven days. This experiment was repeated with similar results. There was a slight difference in time due to a difference in temperature, but the variation was in the same direction. The degree of infection was not, however, different in the two cases.

It seems in the foregoing cases that the temperature employed, whether high or low, was sufficiently favorable to permit of the maximum amount of spore germination, or at least these temperatures allowed about the same percentage of germination; otherwise there would be a difference in the number of infections, unless we assume an alteration in the capacity of the fungi to cause infection or of the hosts to resist it. The latter seems less feasible because it would be a remarkable coincidence if there should be a shift of virulence or susceptibility in such an exact ratio that we would have the same number of infections even though there were a shift in the percentage of germination, especially when we are dealing with two different host plants as well as two pathogens.

Mains (20) by altering the humidity during the incubation period obtained more infection on corn by *Puccinia sorghi* Schw. under high humidity than under low. He employed only 12 hours as an infection period and it is possible that there would have been more infection where the plants were under low humidity had the infection period been extended.

CONDITIONS AFFECTING THE INFECTION PERIOD

The light in the infection chamber was much reduced. First, because the inner chamber was partially constructed of wood; second, the light that reached the plants passed through two panes of glass; and third, the source of light was the diffused light of the headhouse. (It would have been desirable for the inner chamber to have been of glass, but such a chamber was not available.) Whether this subdued light for a period of twelve hours was sufficient to alter the relation of host and parasite can not be stated from our present knowledge. It would be expected to affect the host more than the parasite, because of the autotrophic character of the host. Furthermore if this diffused light had any effect in the short

period of time during which the plants were in the infection chamber it would be to reduce the photosynthetic processes. The reduced food would probably affect only the last stages of infection, after the germ tube had penetrated the host and the energy of the spore was exhausted or reduced. On the other hand the assumption might be made that there is an alteration in the susceptibility of the host, due to a disturbance of an osmotic or chemical equilibrium. The usual time required for starch to be removed from the plant in total darkness seems to indicate that there would be no actual food shortage.

TABLE 1

Record of infection in total darkness as compared with the light of the headhouse in case of bean and buckwheat and the greenhouse in case of wheat

DATE OF INOCULATION	HOST PLANT	LIGHT		DARKNESS		REMARKS
		Plants infected	Plants wilted	Plants infected	Plants wilted	
July 27, 1917.........	Bean	3–3	3–3	3–3	3–3	No apparent difference
July 28, 1917.........	Bean	3–3	3–3	3–3	3–3	No difference
		Plants infected	Total number of spots	Plants infected	Total number of spots	
August 6, 1917.......	Buckwheat	3–3	28	3–3	28	The number of plants infected and the number of spots are the criteria for the amount of infection
August 28, 1917......	Buckwheat	3–3	300	3–3	250	
February 24, 1918....	Buckwheat	3–3	230	3–3	295	Under plants infected 3–3 indicates that three out of three plants were infected
January 25, 1918....	Wheat	23–24		19–21		
January 28, 1918....	Wheat	13–14		13–14		

Some experiments (table 1) were conducted to show whether total darkness as compared with the light of the greenhouse in one case and the light of the headhouse in two other cases alters the total infection of the host plants employed, under the conditions of the experiments. The following pathogens and host plants were used in the experiments: *Colletotrichum lindemuthianum* (Sacc. & Magn.) Bri. and Cav. on bean (*Phaseolus vulgaris* L.); *Ascochyta fagopyrum* Thuen. et Boll. on buckwheat (*Fagopyrum esculentum* Moench.); *Puccinia graminis* Pers. on wheat (*Triticum sativum* Lam.). Both the bean and buckwheat experiments were

conducted in the headhouse mentioned above. In each experiment three plants were placed under a bell jar covered with black paper and three under a jar not so covered. The jars stood on a table before a window. The reason for using the headhouse instead of the greenhouse was that in the latter, during the time in which the experiments were running, the sunlight became so intense at times that under the high humidity of the bell jars the plants were liable to injury. The wheat experiments were performed in the greenhouse during the winter months when the sunlight was not so intense; in fact, cloudy weather prevailed most of the time. The other conditions of the wheat experiments were the same as those mentioned above except that there were more plants used. The experiments were repeated in each case and were run for twenty-four hours, after which the plants were removed to the greenhouse, where they remained until infection became evident. The temperature range was largely between 70 and 80° F. The results are represented in table 1.

It seems fairly safe to conclude from these experiments that light in the infection chamber is not a limiting factor in case of the plants used. It is possible, however, that at the border temperatures and humidities light may manifest itself as a limiting factor.

The carbon dioxide relation

When plants are placed in a closed chamber there is an accumulation of carbon dioxide whenever it is not used up by photosynthesis. The extent of this accumulation depends upon the tightness of the chamber and the amount of circulation provided. The question arises as to whether the concentration of the carbon dioxide becomes sufficiently great in the infection chamber to become deleterious to the host and parasite. If there is an injurious effect, it is possible that the effects are the same in both host and parasite, in which case there probably would be no change in the number of infections. There would be a greater accumulation of carbon dioxide at the higher temperatures, at least until the optimum for respiration was reached, and consequently the effects would be more serious than at low temperatures.

The chambers were not perfectly air-tight. This was indicated by the fact that whenever the electricity was cut off from the heating coils the fall in temperature was sufficiently rapid to show some interchange of air between the inside and outside of the chamber. The greater the differences in temperature on the inside and outside, the greater would be the exchange consequently the tendency for accumulation of CO_2 at high temperatures would be compensated for (at least in part). It would seem therefore that the source of error from carbon dioxide injury would be slight if not negligible.

Influence of sudden change of temperature

When the host plant and pathogen are introduced into the infection chamber they are subjected to a more or less sudden change of temperature, especially when working at low temperatures.

A number of investigators have studied the influence of a sudden change of temperature upon growth in flowering plants, with contradictory results. Sachs (26) and Pedersen (22) conclude that the growth curve follows closely that of temperature. Koeppen (15), Askenasy (3), True (30), Price (23), and Lehenbaur (16) claim that the change itself has a temporary effect, the time varying from one-half to three hours, depending upon the investigator and the amount of change. The evidence seems to be in favor of the latter conclusion. How much this temporary effect may influence infection is not known. Eriksson (9) exposed aeciospores of *Puccinia graminis* to a temperature of 3°C. for two hours and then raised the temperature to about 20°C. He claims that such a change has a beneficial effect and increases the percentage of germination. Melhus (21) found that intermittent temperatures, whether changing from high to low or vice versa, tend to slightly check germination, but suggests that the small variation may be due to experimental error.

Duff (6) found that urediniospores of *Cronartium ribicola* F. de Wal. (which become less viable with age and lose their power of germination in four weeks) which were placed in a refrigerator two weeks after collection germinated only in a small percentage, but a reduction in temperature stimulated a large increase in germination. Spores subjected to a sudden change of temperature three weeks after being collected were stimulated to a slight degree to germinate.

The control of temperature and humidity

On the whole, with the size of the chambers employed the temperature can be kept within a variation of 1°F. The constancy of the temperature is greatly facilitated by the double chamber arrangement with two heating systems and by the use of fans both in the inner and outer chambers.

The temperature control was limited by outside conditions. The chambers were situated in a potting room of a greenhouse where it was possible to maintain a fairly low uniform temperature during the winter. The temperature of the room could be altered by ventilation and the use of steam radiators. This arrangement was sometimes convenient when working at higher temperatures.

The control of humidity was accomplished by means of open pans of

water or saturated salt solutions in combination with temperature manipulations.

Humidities above 95 per cent were difficult to attain whenever the temperature on the inside of the chambers was much higher than that of the outside air, because of inequalities in temperature in the outside chamber. This difficulty was partly overcome by the use of an electric fan and by placing beakers of water on the heating coils. A device was developed during the later stages of the investigation by which it was possible to maintain a saturated condition of air. Instead of using the air heating coils as a source of heat a water heating coil was placed in an evaporating pan containing water, thus insuring a slightly higher temperature of the evaporating surface than of the air and consequently a saturated atmosphere.

Whenever a lower humidity than 95 per cent was desired saturated salt solutions were used. An excess of salt insured a definite vapor pressure at a given temperature and hence a constant humidity. The wide range of vapor pressure of saturated salt solution made it possible to obtain almost any humidity desired.

It is not possible to predict the exact humidity that will result from a given saturated solution. First, because the vapor pressure of the majority of saturated solutions has not been worked out for the various temperatures; second, the vapor pressure of the entire system is altered by the introduction of plants. The leaf surface presents an evaporating surface very near that of pure water, tending to increase the humidity of the system. However, as soon as the system comes to an equilibrium, the humidity becomes constant. It is possible by the inspection of the vapor pressure of the various salts at a given temperature to predict what salt to employ in order to obtain an alteration in humidity in the desired direction. The humidities obtained from the various salts vary in the same direction as the vapor pressures of those salts. Some of the salts used are as follows:—Potassium sulphate with a vapor pressure of the saturated solution of 17.21 mm. mercury at 20°C., Barium chloride V.P. at 20°C. 15.45, Sodium nitrate V.P. at 20°C. 13.7 mm., Cadmium chloride V.P. at 20°C. 12.2 mm.

Relative humidity as a unit of comparison

As has been pointed out by Livingston and others, relative humidity is not a satisfactory unit of comparison whenever more than one temperature is employed. Livingston (18) suggests the use of vapor pressure deficit, which equals the difference between the maximum vapor pressure of water vapor at a given temperature and the actual pressure of water vapor in a given space at a given temperature.

METHODS AND MATERIALS

The following pathogens and host plants were employed in these experiments: *Collectotrichum lindemuthianum* (Sacc. & Magn.) Bri. & Cav. on red kidney bean (*Phaseolus vulgaris* L.) *Puccinia graminis* Pers. var. *tritici* Erick on wheat (Triticum), and *Ascochyta fagopyrum* on buckwheat, gray variety, (*Fagopyrum esculentum* Moench.). The fungi employed were all pure line strains to which the respective hosts were susceptible. An attempt was made to secure pure line strains of the host but this could not be done except in the case of wheat.[3]

The bean and buckwheat plants were grown in two inch pots and the wheat in an inch and a quarter pots in a greenhouse with a temperature ranging from 60° F. to 85° F. and relative humidity varying from 60 per cent to 85 per cent.

Plants of the same age were used as far as possible. Some variation was inevitable, however, even under greenhouse conditions. The beans were usually from sixteen to twenty days old, the wheat from seven to ten, and buckwheat from twenty to twenty-four days old. An effort was likewise made to use spores of the same age. Here some variation occurred, due to the necessarily different conditions under which the organisms were grown. Colletotrichum was grown on bean pods, Ascochyta on potato agar, and the spores of *Puccinia graminis* obtained directly from pustules on the host plant.

Twenty pots were used in each experiment, with one plant in each pot, except in case of wheat, where the number of plants varied from three to five. These cultures were divided into five series of four pots each and designated by the following symbols: Ch 1, Ch 2, Ch 3, F, and D. The plants in Ch 1 were taken directly from the greenhouse when the particular experiment was started, and placed in the infection chamber. The purpose of this series was to show whether or not any infection that occurred was due to spores that may have come in contact with the host before inoculation. The remaining four series were sprayed with a spore suspension from an atomizer (except in case of wheat) and used as follows. The plants in Ch 2 were placed in a special chamber at temperatures and humidities known to be favorable for the development of the disease. This procedure was to determine whether the spores were viable and whether infection would take place if conditions were favorable. The plants of Ch 3 were dried immediately by means of an electric fan and left in the greenhouse as a check to show whether infection occurred

[3] The wheat seed for these experiments was furnished by Dr. E. C. Stakman. This strain was given the number 169 by him and was used because of its susceptibility to the attack of *Puccinia graminis*.

in the infection chamber or in the greenhouse. Series F consisted of plants placed in the infection chamber directly after inoculation and covered with a water suspension of spores. In series D the plants were dried at once and placed in the infection chamber. This series was employed to determine whether a film of water over the surface of the plants was essential to infection. Sometimes series D was omitted in the temperature experiments.

TABLE 2

Record of amount of infection on wheat plants by Puccinia graminis tritici at various low temperatures, the humidity being practically constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	RELATIVE HUMIDITY	EXTENT OF INFECTION			
				F[1]	Ch. 1[1]	Ch. 2[1]	Ch. 3[1]
				Number of plants infected	Number of plants infected	Number of plants infected	Number of plants infected
December 18, 1917.....	53.0–52.6	0.4°	97.5	12–34[2]	0–17	17–18	0–16
December 19, 1917.....	53.0–52.6	0.4°	97.5	8–28	0–20	14–24	0–16
December 31, 1917.....	52.7–52.2	0.5°	97.0	9–43	0–24	22–25	0–16
December 21, 1917.....	51.7–51.2	0.5°	97.0	23–43	0–18	16–22	0–20
January 3, 1918.....	50.8–50.4	0.4°	97.0	2–30	0–15	18–22	0–14
January 10, 1918.....	49.8–49.75	0.05°	99.0	5–44	0–18	19–20	0–17
December 10, 1917.....	47.2–46.7	0.5°	96.0	0–30	0–16	16–19	0–12
January 6, 1918.....	47.1–46.75	0.35°	97.0	2–44	0–16	19–20	0–16
December 11, 1917.....	47.0–47.0	0.0°	100.0	1–40	0–20	17–25	0–22
January 19, 1918.....	46.85–46.75	0.1°	99.0	1–41	0–22	25–35	0–22
January 22, 1918.....	46.48–46.2	0.28°	98.0	7–35	0–16	27–27	0–16
January 21, 1918.....	45.5–45.3	0.2°	98.0+	5–31	0–17	12–24	0 26
December 14	42.2–42.0	0.2°	98.0+	0–38	0–20	23–23	0–14

[1] An explanation of symbols is given on page 17.

[2] In this table the number of diseased plants is the criterion of infection. 12–34, 0–17, 17–18, 0–16, etc., means that 12 out of 34 plants, 0 out of 17, etc., were infected.

The wheat was inoculated by removing the spores from pustules of diseased leaves by means of a scalpel and spreading them on the wheat leaves. Ch 2 and F were then sprayed with water from an atomizer.

The plants were allowed to remain in the infection chamber for twenty-four hours and were then returned to the greenhouse, where they remained until the disease developed. The time for the development of the disease varied somewhat with the greenhouse conditions, but since the time is influenced little during the infection period it was not considered in recording data. Sufficient time was allowed in each case for any possible infection to become manifest. Bean plants were allowed ten to fourteen days, wheat thirteen to twenty, and buckwheat ten to fifteen days.

An electric fan was placed in the greenhouse in such a position as to blow a current of air between and above the plants in order to prevent the accumulation of higher humidities immediately around the plants. This procedure was found necessary in some instances to prevent infection of buckwheat. The bean and wheat never showed any tendency to the development of the diseases in the greenhouse. In one instance Ch 3 plants showed infection in case of wheat.

TABLE 3

Record of infection on buckwheat plants by Ascochyta fagopyrum at various low temperatures, the humidity remaining practically constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	RELATIVE HUMIDITY	EXTENT OF INFECTION[1] F: Number of plants infected	F: Total number of lesions	Ch. 1: Number of plants infected	Ch. 2: Number of plants infected.	Ch. 2: Total number of lesions	Ch. 3: Number of plants infected
December 21, 1917	59.50–59.15	0.35°	98.0	7–8	52	0–4	4–4[2]	Numerous	0–4
December 22, 1917	56.70–56.10	0.6°	96.0	0–8	0	0–4	4–4[3]	43	0–4
December 19, 1917	56.10–55.40	0.7°	95.5	2–9	4	0–4	4–4	55	0–4
January 14, 1918...	54.25–54.18	0.07°	99.0	1–8	1	0–4	4–4	60	0–4
January 7, 1918...	53.25–53.00	0.25°	98.5	1–8	1	0–4	4–4	20	0–4
December 11, 1917	48.40–48.00	0.4°	97.0	0–8	0	0–4	4–4	32	0–4
January 22, 1918...	46.48–46.1	0.38°	97.0	4–8	15	0–4	4–4	100	0–4
January 21, 1918...	45.60–45.35	0.25°	98.5	1–8	3	0–4	4–4	150	0–4
December 13, 1917	42.80–42.60	0.2°	98.5	0–8	0	0–4	4–4	Numerous	0–4
December 10, 1917	41.70–40.65	1.05°	92.0	0–6	0	0–4	4–4	36	0–4
December 14, 1917	38.00–37.80	0.2°	98.5	0–8	0	0–4	4–4	All dead	0–4

[1] Two methods of measuring the amount of infection are employed in this table, for example, in column 1 under F the number of diseased plants is used as a basis, while in column 2 the total number of lesions occurring on all the plants marked F are given.

[2] All plants were wilted.

[3] Infection on primary leaves only, 3 plants wilted, one leaf of remaining plant wilted.

Influence of low temperature upon infection of wheat

From table 2 it will be seen that wheat can become infected by *Puccinia graminis* at a temperature as low as 45.5° F. but the infection is very slight and rapidly decreases at temperatures below 45.5° F. In the single experiment run at 42° F. there was no infection. This experiment should

TABLE 4

Record of infection on bean plants by Colletotrichum lindemuthianum at various low temperatures, the humidity remaining constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	RELATIVE HUMIDITY	EXTENT OF INFECTION					
				F		Ch 1	Ch 2		Ch 3
				Number of plants infected	Description of infection	Number of plants infected	Number of plants infected	Description of infection	Number of plants infected
January 28, 1918.....	63.8–63.6	0.2°	98.5	8–8	1 plant wilted, 40 per cent of veins colorized, lesions mostly large, 3 to 4 cm. in length	0–3	4–4	3 leaves wilted, 60 per cent coloration	0–4
January 30, 1918.....	62.9–62.5	0.4°	97.3	7–8	1 plant wilted, 1 leaf of each of 2 other plants wilted, 40 per cent coloration, lesions large	0–3	4–4	All plants wilted	0–4
January 21, 1918.....	61.6–61.2	0.4°	97.3	1–8	1 lesion	0–4	4–4	3 plants wilted, 1 leaf of remaining plant wilted, 5 lesions on remaining leaf	0–4
January 22, 1918.....	59.7–59.1	0.6°	96.0+	3–8	22 lesions	0–4	4–4	2 plants wilted, lesions numerous. Lesions 1–2.5 cm. in length	0-4

January 25, 1918.....	61.3–60.6	0.7°	96.0	0–8		0–4	4–4	1 plant wilted, 1 leaf of each of 2 remaining plants wilted, 40 per cent coloration of remaining leaves	0–4
January 17, 1918.....	59.1–58.6	0.5°	97.0	0–8		0–4	4–4	2 leaves wilted, 1 additional leaf wilted. Lesions large, 2 to 4 cm. long. 33 additional lesions	
December 31, 1917...	57.9 –57.3	0.6°	96.0	3–8	Infection on 2 plants limited to secondary leaves (11 lesions), 12 lesions on primary leaves of third plant	0–4	4–4	All the plants wilted	0–4
January 8, 1918......	54.85–54.7	0.15°	98.8	0–8		0–4	4–4	All the plants wilted	0–4
January 7, 1918......	53.3–53.1	0.2°	98.5	0–8		0–4	4–4	3 plants wilted. Fourth plant partially wilted	0–4

at least have been duplicated but the low temperature did not prevail at the time. However, the humidity was very favorable and the infection between this point and 50° F. was very slight. It seems therefore that 45° F. is near the lower limit of infection. This point is only about 9° F. above the lowest temperature at which Johnson (13) was able to obtain germination of spores of *Puccinia graminis.*

The amount of infection rises rapidly from within a few degrees of the lower limit to almost a fair average for the higher temperatures, indicating that there is no definite optimum temperature for infection. These results correspond to those obtained by Johnson (13) for germination of spores of *Puccinia graminis.* He found no definite optimum temperature when percentage germination was used as a basis for measuring the amount of germination.

Influence of low temperatures upon infection of buckwheat by Ascochyta fagopyrum

No infection was obtained in buckwheat below 45.5° F (table 3). Another experiment at 42° F. and at high humidity should have been conducted as a further check upon the lower limit but the outside temperature was not sufficiently low to do so. Some variation in the amount of infection between 45° F. and 59° F. will be noted, and even an absence of infection in some cases. An observation of a certain phenomenon in connection with spore germination of the pathogen suggests a possible explanation of this variation. At times, and for reasons unknown, the fungus produced one-celled spores. Whether these spores are merely immature spores is not known, because old cultures sometimes contain them. These spores do not germinate nearly as well as the two-celled spores. At higher temperatures, however, they seem to produce infection. It is possible that these spores may fail to produce infection as the temperature becomes less favorable. This problem needs to be solved.

Low temperatures and infection of bean by C. lindemuthianum

From table 4 it will be seen that the lower limit for infection of bean by Colletotrichum is 57° F. where the plants remain in the infection chamber for twenty-four hours. It is possible that if this time were extended, a lower limit might be obtained.

The rise in the amount of infection here as in case of wheat and buckwheat is rapid. Excellent infection was secured at 63° F.

Infection of wheat at higher temperatures by P. graminis tritici

The highest temperature at which *Puccinia graminis* will produce infection in wheat (table 5) is 80° F., at least under the conditions of the experiment. This temperature is 7.8° F. below the maximum at which the spores will germinate. It is possible that in a saturated atmosphere this temperature might be raised. It seems probable, however, that the highest temperature at which infection will take place is below the maximum for germination.

TABLE 5

Record of infection on wheat plants by Puccinia graminis at various high temperatures, the humidity remaining practically constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	HUMIDITY READINGS	EXTENT OF INFECTION[1]				
				F	D[2]	Ch. 1	Ch. 2	Ch. 3
				Number of pots in which infection occurred	Number of pots in which infection occurred	Number of pots in which infection occurred	Number of pots in which infection occurred	Number of pots in which infection occurred
August 25, 1917	82.4–81.70	0.7°	97.0+	0–4	0–4	0–4	4–4	0–4
September 3, 1917	82.0–81.30	0.7°	97.0+	0–4	0–4	0–4	4–4	0–4
August 28, 1917	81.5–81.10	0.39°	98.5	0–4	0–4	0–4	4–4	0–4
September 28,1917	80.8–80.00	0.8°	97.0	0–4	0–4	0–4	4–4	0–4
September 24, 1917	80.0–79.10	0.9°	96.0+	0–4	1–4	0–4	4–4	0–4
September 27, 1917	80.0–79.00	1.0°	96.0	1–4	0–4	0–4	4–4	0–4
September 29, 1917	78.0–77.00	1.0°	96.0	1–5	1–2	0–4	4–4	0–4

[1] In these experiments the number of plants diseased was not counted (there being 3 to 5 plants in each pot), but the number of pots in which infection occurred was used as basis of measurement.

[2] Explanation of symbols is given on page 17.

Infection of bean at higher temperatures by C. lindemuthianum

The highest temperature at which infection took place in bean was 80° F. (table 6). With both wheat and bean a large number of experiments were run at temperatures above 80°. The increase in the number of plants infected was rapid as the temperature was lowered. The range covered is not sufficient to show the same decided increase in the amount of infection. One finds this suggestion, however, in the data.

This maximum temperature for infection falls 7.8° F. below the temperature at which Edgerton finds Colletotrichum to grow in culture media.

TABLE 6

Record of infection on bean plants by Colletotrichum lindemuthianum at various high temperatures, the humidity remaining practically constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULK	RELATIVE HUMIDITY	EXTENT OF INFECTION							
				F		D		Ch 1	Ch 2		Ch 3
				Number of plants infected	Description of infection	Number of plants infected	Description of infection	Number of plants infected	Number of plants infected	Description of infection	Number of plants infected
August 6, 1917......	83.3 –82.6	0.7°	97	0–4		0–4		0–4	4–4	All plants wilted	0–4
August 7, 1917......	83.25–82.75	0.5°	98	0–4		0–4		0–4	4–4	All plants wilted	0–4
August 13, 1917.....	83.3 –82.5	0.8°	96+	0–4		0–4		0–4	4–4	All plants wilted	0–4
August 25, 1917.....	82.3 –81.7	0.6°	98−	0–4		0–4		0–4	4–4	Infection fair	0–4
September 3, 1917...	82.0 –81.3	0.7°	97	0–4		0–4		0–4	4–4	All plants wilted	0–4
August 28, 1917.....	81.5 –81.1	0.4°	98+	0–4		0–4		0–4	4–4	2 leaves partly wilted, coloration throughout veins	0–4
September 17, 1917..	81.0 –80.9	0.1°	99+	2–4	In 1 plant 2 spots on secondary leaves, 1 spot on primary leaf. Second plant large number spots on secondary leaves. Several large spots on 1 leaf	0–4		0–4	4–4	Some dead areas. All the veins colorized	0–4

September 24, 1917..	80.4 –79.1	1.3°	95	1–4		1–3	2 spots on secondary leaves. 1 on primary	0–4	4–4	Infection medium, 4 leaves partly wilted	0–4
September 26, 1917..	80.0 –79.0	1.0°	96	2–4	8 lesions on primary leaves	3–4	1 case infection confined to secondary leaves. On other 2 plants infection on primary leaves. 1 leaf 1 spot. Other plant several lesions	0–4	4–4	All wilted	0–4
September 28, 1917..	80.8 –80.0	0.8°	97	1–4	7 small lesions	1–4	2 lesions on secondary leaves	0–4	4–4	3 completely wilted, fourth badly infected	0–4
September 29, 1917..	78.0 –77.0	1.0°	96	4–4	Lesions largely confined to secondary leaves	4–4	Largely confined to secondary leaves	0–4	4–4	3 plants completely wilted	0–4

Infection of buckwheat at higher temperatures by Ascochyta fagopyrum

The upper limit for the growth of buckwheat appears to be about 100° F. (table 7). Most of the plants collapsed after having been in the infection chamber at this temperature for twenty-four hours. Yet in one instance typical Ascochyta lesions appeared on plants that survived. I have germinated the spores of the fungus at a temperature of 106° F. The maximum temperature for germination has not been determined. Some ex-

TABLE 7

Record of infection of buckwheat by Ascochyta fagopyrum at various high temperatures and within the humidity range at which infection takes place

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	RELATIVE HUMIDITY	EXTENT OF INFECTION							
				F		D		Ch. 1	Ch. 2		Ch. 3
				Number of plants infected	Total number of lesions	Number of plants infected	Total number of lesions	Number of plants infected	Number of plants infected	Total number of lesions	Number of plants infected
			per cent								
March 12, 1918....	100.0–100.0	0°	100.0	2–11[1]	2	—	—	0–4[2]	4–4	37	0–4
March 13, 1918....	100.0–100.0	0°	100.0	0–8[3]	0	—	—	0–4[4]	4–4	119	0–4
August 3, 1917.....	97.7– 95.2	2.5°	91.5	1–4	Several	1–4	Few	0–4	4–4	Numerous	2–4[5]
September 27, 1917	93.3– 90.8	2.5°	91.5	1–4	1	1–4	3	0–4	4–4	90	0–4
September 28, 1917	92.6– 90.3	2.3°	92.0	1–4	5	1–4	2	0–4	4–4	24	0–4
September 6, 1917	91.0– 88.0	3.0°	89.0	3–4	10	1–4	2	0–4	4–4	117	0–4

[1] Four out of 11 plants were dead. Remaining were all injured.
[2] All 4 plants were dead at end of infection period.
[3] Seven out of 8 plants were dead.
[4] Two plants dead; 2 remaining plants injured.
[5] These plants show infection but they were at the end of the greenhouse, where there was dropping from the roof.

periments were conducted at temperatures above 100° F., but the plants always died.

The limits of temperature at which infection by Ascochyta occurred in buckwheat were wider than in wheat and bean. In the latter two the maximum temperatures for growth are higher than for infection. It is possible, at least in case of beans, to grow them at temperatures unfavorable for the fungus and thus escape the losses due to this disease where the other conditions for its development are favorable.

Infection of buckwheat at various humidities by Ascochyta fagopyrum

In table 8 is shown the infection of buckwheat at various humidities, the temperature remaining nearly constant. The lowest humidity at which infection has been observed to take place on buckwheat is 91 per cent. The humidity rises to 94.5 per cent where the plants were dried before placing them in the chamber. It will be noted, however, that considerable infection took place at this humidity. This table not only shows that infection can take place at the temperatures considered, within a

TABLE 8

Record of infection on buckwheat by Ascochyta fagopyrum at various humidities, the temperature remaining practically constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	RELATIVE HUMIDITY	EXTENT OF INFECTION							
				F		D		Ch. 1	Ch. 2		Ch. 3
				Number of plants infected	Total number of lesions	Number of plants infected	Total number of lesions	Number of plants infected	Number of plants infected	Total number of lesions	Number of plants infected
November 15, 1917	77.1–76.2	0.9°	96.3	3–4	23	3–4	11	0–4	4–4	32[1]	0–4
November 20, 1917	77.6–76.3	1.3°	95.0+	2–3	12	3–4	17	0–4	4–4	57	0–4
November 13, 1917	78.0–76.0	2.0°	91.0	1–4	2	0–4	0	0–4	4–4	54	0–4
November 8, 1917	78.7–76.9	1.8°	91.5	0–4	0	0–4	0	0–4	4–4	100	0–4
November 27, 1917	77.3–75.2	2.1°	90.6	2–4	4	0–4	0	0–4	4–4	55	0–4
October 4, 1917	77.1–74.5	2.6°	89.0	0–4	0	0–4	0	0–4	4–4	37	0–4
October 8, 1917	77.2–74.7	2.5°	89.0	0–4	0	0–4	0	0–4	4–4	46	0–4

[1] Plant wilted (lesions not counted).

range from 91 per cent to 100 per cent humidity, but that a film of water covering the leaf surface is not essential to infection.

The question may arise as to the possible presence of a film on the leaf surface at such high humidities. It has been observed throughout these experiments that plants placed in the chamber with a film covering the leaf surface are dry when removed at the end of twenty-four hours. Since the chamber is always run at a temperature above that of the surrounding atmosphere, evaporation must always take place because under these conditions saturation is rarely ever reached. The only cases where a condition of saturation has been observed are at the lowest temperatures.

Infection of wheat at various humidities by P. graminis tritici

The range of humidity for infection in wheat (table 9) is a little narrower than it is for buckwheat. The lowest humidity at which infection has been observed is 95 per cent. No infection takes place at 92 per cent and below. The same general difference is observed between the plants with a film and those without. The dry plants require a slightly higher humidity.

TABLE 9

Record of infection of wheat by Puccinia graminis tritici at various humidities, the temperature remaining practically constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	RELATIVE HUMIDITY	EXTENT OF INFECTION				
				F	D	Ch. 1	Ch. 2	Ch. 3
				Number of plants infected	Number of plants infected	Number of plants infected	Number of plants infected	Number of plants infected
February 18, 1918	70.0–69.6	0.4°	98+	12–15	15–17	0–27	22–22	0–25
March 7, 1918	68.9–68.4	0.5°	97	5–22	5–17	0–26	14–18	0–17
March 8, 1918	68.2–67.3	0.9°	96	5–16	2–19	0–16	10–15	0–13
February 24, 1918	67.5–66.7	0.8°	96−	8–19	3–16	0–20	28–29	4–24[1]
March 4, 1918	68.9–67.9	1.0°	95	7–16	3–13	0–15	10–11	0–12
March 10, 1918	68.0–67.0	1.0°	95	6–17	0–17	0–18	8–11	0–17
November 17, 1917	68.0–66.5	1.5°	93	0–16	0–15	0–17		0–14
November 22, 1917	68.2–66.7	1.5°	93	0–15	0–14	0–12	12–17	0–14
November 28, 1917	68.5–67.0	1.5°	93	0–15	0–15	0–15	14–18	0–14
November 12, 1917	68.1–65.6	2.5°	88	0–20	0–17	0–18	12–16	0–19
December 3, 1917	68.0–65.3	2.7°	88	0–14	0–16	0–17	11–15	0–13

[1] In this case Ch 3 showed slight infection, the only case ever recorded on wheat.

The temperatures at which the humidities were studied were arbitrarily selected, after considerable preliminary work. These temperatures were thought to be within the limits of the optimum.

Influence of humidity upon infection of bean by Colletotrichum lindemuthianum

The lowest humidity at which infection took place in bean is near that of wheat. The data in table 10 do not show any infection at 95 per cent humidity, but only one experiment was run at this humidity. Negative results were also obtained with wheat at 95 per cent humidity.

TABLE 10

Record of infection by Colletotrichum lindemuthianum on bean at various humidities, the temperature remaining nearly constant

DATE OF INOCULATION	PSYCHROMETER READINGS FAHR. SCALE	DEPRESSION OF WET BULB	RELATIVE HUMIDITY	EXTENT OF INFECTION: F — Number of plants infected	F — Extent of infection	D — Number of plants infected	D — Extent of infection	Ch 1 — 1	Ch 1 — Number of plants infected	Ch 2 — Extent of infection	Ch 3 — Number of plants infected
March 16, 1918......	68.7–68.3	0.4°	97.0	4–4	Leaves wilting around discolored veins. Many lesions	4–4	Veins colored pink. 150–200 lesions	0–4	4–4	All dead	0–4
March 24, 1918......	69.0–68.5	0.5°	97.0	4–4	1 plant badly wilted. Veins colored 200 lesions	4–4	Veins colored. Leaves wilting. Many lesions.	0–4	4–4	All dead	0–4
March 20, 1918......	67.4–66.8	0.6°	96.6	5–5	50 per cent coloration. 49 lesions	2–4	2 lesions. 1 on each plant	0–4	4–4	2 plants dead. A leaf of each on 2 additional plants wilted. Numerous lesions	0–4
March 23, 1918......	68.2–67.6	0.6°	96.6	3–4	12 lesions on 1 plant. 2 leaves wilted on 2 plants. Also many lesions	4–4	1 leaf partly wilted on each of 2 plants. 2 lesions on 1 plant. Many lesions on other two	0–4	4–4	Leaves covered with lesions. 60 per cent coloration of veins	0–4
March 22, 1918......	69.0–68.2	0.8°	95.8	4–4	2 plants 1 lesion each. 1 plant 108 lesions. 1 plant 167 lesions.	1–4	8 lesions	0–4	4–4	Lesions numerous 70 per cent of veins colored	0–4
November 23, 1917..	68.9–68	0.9°	95.0+	0–4		0–4		0–4	4–4	All dead	0–4
November 17, 1917..	68.0–66.5	1.5°	93.0	0.4		0–4		0–4	4–4	2 plants wilted. 2 partially wilted	0–4
November 28, 1917..	68.5–67	1.5°	93.0	0–4		0–4		0–4	4–4	All wilted	0–4
December 3, 1917....	68.0–65.3	2.7°	86.8	0–4		0–4		0–4	4–4	All wilted	0–4
December 6, 1917....	67.5–64.8	2.7°	86.8	0–4		0–4		0–4	4–4		0–4

A large number of experiments were run at humidities above 95 per cent. The data given in the table are representative of the results obtained. A large number of experiments were conducted at humidities of 92 per cent and below.

There is a rapid rise in the number and extent of infections from 95 per cent up to 100 per cent. At 97 per cent humidity, the highest humidity given in the table, the amount of infection approaches closely that in Ch 2, where saturation was attained at least part of the time and where the film over the leaf was maintained throughout the infection period due to precipitation because of alterations in temperature. The temperatures in Ch 2 varied largely between 65° F. and 75° F. The same influence of the presence of a film is to be noted as in the wheat and buckwheat.

DISCUSSION AND CONCLUSIONS

Heretofore the study of the effects of temperature upon the relation of parasite to host has been limited largely to the influence of temperature upon the growth of the fungus and the germination of the spores. In a few cases the effects of temperature upon the development and extension of diseased tissue has been studied (Ball (4), Brooks and Cooley (5)). This phenomenon is largely one of growth and seems to obey, in the main, the Van't Hoff law. The growth of the fungus behaves in the same way (Tisdale (29), Brooks and Cooley (5)).

A number of methods have been employed to measure the effect of temperature upon germination, with varied results. In some cases it would seem that all the factors involved were not considered.

The extension of the germ tube and the development of mycelium have been used as a basis for the study of the influence of temperature upon germination and infection (Johnson, E. C. (13), Wiesner (30), Balls (4), etc.). Here one is dealing with a growth phenomenon, and when food is not a limiting factor one would expect the behavior of this phenomenon towards temperature to be the same as found among flowering plants and the growth of fungi in culture media. For every increase of 10°C. (within certain limits) there would be a doubling or trebling of growth in a given time (Tisdale (29), Brooks and Cooley (5), Edgerton (7)).

The time required for germination has been used as a measure of the influence of temperature. The results have been rather uniform, and there has been a general shortening of time with an increase of temperature to a more or less optimum temperature in the same proportion as demanded by the Van't Hoff law (Anderson (1), Hecke (12), Wiesner (31), Ravaz (24), Melhus (21), Shapovalov (27)). Ames (2) obtained varied results with different species. In some cases the optimum is very broad,

while in others the time is shortened with an increase of temperature to a rather definite optimum.

Where percentage germination has been used as a criterion for measuring the effects of temperature, fairly uniform results have been obtained. The optimum, as a rule, is broad, as one would naturally expect if sufficient time were allowed at the lower temperatures for germination to take place. If a shorter time were used different results might be expected. Melhus' (21) results with the spores of *Phytophthora infestans* show a fairly broad optimum (5° to 13°C.) where he used the number of cultures in which germination occurred as a basis of measurement of the temperature effects. It is sharper, however, than that obtained by other investigators. Where he used the percentage germination in the various cultures as a criterion, there was a gradual rise in percentage from 5° to 13°C. He states, however, that there was a variation from 13 to 80 per cent in germination at the optimum. This fact may account for the difference in the two curves. Ames (2) abandoned percentage as a basis of measuring the effects of temperature upon germination because her results were not uniform. Anderson (1) found the percentage germination of the spores of *Cylindrosporium scoparium* Morg. was almost total between 12° and 30°C., ranging between 95 and 100 per cent. Johnson (13) did not obtain a definite optimum temperature for *Puccinia graminis* by percentage germination, there being no uniformity between 9° and 25°C.

From these results it would seem that the number of spores which germinate does not rise with an increase in the temperature to a definite optimum, but that the range at which a large number of spores will germinate is wide. One would expect, then, that there would be a wide range of temperature at which the number of infections that would take place would not vary much if sufficient time were allowed for the spores at lower temperatures to cause infection, providing some other factor did not enter in. This view corresponds to the results of the present experiments (tables 2, 3, and 4). Some experiments were conducted between the temperature limits given in the tables with results which conform to this conclusion. These results have also been confirmed by Ravn and Fromme (pages 11 and 12).

An understanding of this phenomenon is important wherever the number of lesions, such as in leaf spots, fruit spots, etc., is responsible for the chief loss due to diseases. If there were a definite optimum, the number of lesions that would develop would gradually decline as the temperature was lowered from the optimum. The infection phenomenon viewed in this light implies a different attitude towards control measures. Not only must the degree of temperature be considered, but the time to which the host plant is exposed to conditions of infection, in connection with

the number of infections that take place as well as the development and extension of a particular lesion.

Some incidental data obtained in the present investigation in connection with infection of bean by *C. lindemuthianum* near the lower temperature limit indicate that the time element is important. The data point to a lower temperature limit for infection where forty-eight hours were used for an infection period than where twenty-four hours were used.

From the data presented, an interesting relation between host and parasite is brought out. The temperature ranges for host and parasite are not identical in any of the cases. The temperature range for growth of bean and wheat is wider than for the germination of spores and of infection by *C. lindemuthianum* and *P. graminis*. The maximum temperature for infection by the two pathogens is about the same in the time employed (tables 5 and 6) while the lower limit for infection by *P. graminis* (compare tables 2 and 4) is lower than for infection by *C. lindemuthianum*. The upper temperature limit for the growth of bean is higher than for germination of the spores of and infection by *C. lindemuthianum*, which fact has made possible the control of anthracnose in the Southern States. The optimum temperature for the growth of bean is probably higher than that of wheat.

The exact temperature ranges for Ascochyta and buckwheat have not been determined. There is no indication as to which has the wider range. Their ranges do not coincide, because buckwheat is killed at a temperature at which infection takes place and below the maximum temperature for germination of spores of Ascochyta (table 7). These relations are all important in connection with control measures.

The variation in the amount of moisture in the air in different regions is probably important in the distribution of diseases over the earth's surface. The absence of certain diseases in semi-arid and arid regions where agriculture has been practiced for long periods of time may be due in part to the small moisture content of the air.

Seasonal variation in the moisture content of the air plays an important part in determining the amount of disease that may develop.

In the course of the present investigation (compare tables 8, 9, and 10), a variation in the humidity in the air required for infection for the individual plant has been exhibited. Infection occurred at a slightly lower humidity in buckwheat than in case of bean and wheat. As mentioned earlier, it was necessary to provide for circulation of air about the buckwheat plants to prevent infection in the greenhouse. This same provision was found requisite in a few experiments conducted with *Septoria lycopersici* Speg. on tomato. The tendency for infection to take place in the greenhouse was more marked with tomato than with buckwheat.

The degree of humidity in the general environment of the plant may be an inaccurate criterion of the amount of moisture required for infection, at least when there is little air movement. The air movement created by an electric fan over a bench in the greenhouse has been sufficient to prevent infection of buckwheat by *A. fagopyrum* and of tomato by *S. lycopersici* where in its absence infection took place. The higher humidity in the immediate environment of the plant may be of considerable significance in connection with infection in nature.

Just how the spore upon the plant surface obtains sufficient moisture for germination and infection is an unsolved problem. Within certain limits of humidity, that is, where the evaporation is not too great, the spore is able to absorb sufficient water for germination. The absorption may be from the host plant, at first by imbibition and later by osmosis. It is possible that in the depressions of the leaf surface and especially immediately above the stomata a higher humidity prevails which may afford sufficient moisture for germination.

There is a possible relation to hairiness because the juvenile leaves of buckwheat have more hair than the secondary leaves and seem to be infected more readily (the data contained in the tables are from the secondary leaves). The secondary leaves of the bean are more pubescent and seem to be infected more easily at the limiting humidities. The hair would tend to prevent evaporation and increase the humidity at the leaf surface.

SUMMARY

The lower temperature limit for infection of wheat by *Puccinia graminis tritici* is somewhere near 42° F. The amount of infection rises rapidly and at 53° F. it approaches the average for higher temperatures.

The lower temperature limit for infection of buckwheat by *Ascochyta fagopyrum* is about 45° F. There is some variation in infection between this temperature and 59° F., possibly due to the one-celled spores sometimes produced in culture.

The lower temperature limit for infection of bean by Colletotrichum is about 57° F. This limit may be influenced by the time the plants are in the infection chamber.

The upper temperat re limit for infection of wheat is 80° F.

The maximum temperature for infection of buckwheat by Ascochyta is about 100° F. At this temperature buckwheat plants are injured or killed.

The upper temperature limit for infection of bean is 80° F. With the decrease of temperature there is a rapid increase in the number of plants infected.

There seems to be no definite optimum temperature for infection in the hosts and parasites used where the number of infections is used as a measure of the amount of infection and sufficient time is allowed for the fungi to establish a relation with the hosts.

The range of humidity for infection of buckwheat varies between 90 per cent and 100 per cent. Where the plants are dried off before being placed in the infection chamber, it varies between 94.5 per cent and 100 per cent.

The humidity range for infection of wheat is between 92 per cent and 100 per cent. The lowest humidity at which infection has taken place is 95 per cent. The range for the dried plants is a little narrower.

The range of humidity for infection of bean lies between 92 per cent and 100 per cent.

A film of water covering the leaf surface is not essential to infection.

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LITERATURE CITED

(1) ANDERSON, J. P. Rose canker and its control. Mass. Agr. Expt. Sta. Bul. 183: 7–46. 1918.

(2) AMES, ADELINE The temperature relations of some fungi causing storage rots. Phytopathology **5**: 11–19. 1915.

(3) ASKENASY, E. Ueber einige Beziehungen zwischen Wachsthum und Temperatur. Ber. Deut. Bot. Ges. **8**: 61–94. 1890.

(4) BALLS, W. S. Temperature and growth. Ann. Bot. **22**: 557–591. 1908.

(5) BROOKS, CHARLES, AND COOLEY, J. S. Temperature relations of apple-rot fungi. Jour. Agr. Research **8**: 139–164. 1917.

(6) DUFF, GEORGE H. Some factors affecting viability of urediniospores of Cronartium ribicola. Phytopathology **8**: 289–292. 1918.

(7) EDGERTON, C. W. Effect of temperature on Glomerella. Phytopathology **5**: 247–259. 1915.

(8) EDGERTON, C. W. Effect of temperature on Glomerella. Science n. s. **41**: 174. 1915.

(9) ERIKSSON, J. Ueber die Förderung der Pilzsporenkeimung durch Kälte. Centbl. f. Bakt. II **1**: 557–565. 1895.

(10) FROMME, F. D. The culture of cereal rusts in the greenhouse. Bul. Torrey Bot. Club. **40**: 501–521. 1913.

(11) GILMAN, J. C. Cabbage yellows and the relation of temperature to its occurrence. Ann. Missouri Bot. Gard. **3**: 25–82. 1916.

(12) HECKE, LUDWIG Untersuchungen über Phytophthora infestans De By. als Ursache der Kartoffelkrankheit. Jour. Landw. **46**: 97–142. 1898.

(13) JOHNSON, E. C. Cardinal temperatures for the germination of uredospores of cereal rusts. Phytopathology **2**: 47–48. 1912.

(14) JOHNSON, JAMES Host plants of Thielavia basicola. Jour. Agr. Research **7**: 289–300. 1916.

(15) KOEPPEN, W. P. Wärme und Pflanzenwachsthum. Bul. Soc. Imp. Nat. Moscou 43, 1870: 41–110. 1871.

(16) LEHENBAUER, P. A. Growth of maize seedlings in relation to temperature. Physiological Research **1:** 247–288. 1914.

(17) LEVIN, EZRA The leaf-spot disease of tomato. Michigan Agr. Expt. Sta. Tech. Bul. 25: 1–51. 1916.

(18) LIVINGSTON, B. E. The vapor tension deficit as an index of the moisture condition of the air. Johns Hopkins Univ. Cir. 293: 170–175. March, 1917.

(19) LOCK, R. H. On the growth of giant bamboos with special reference to the relation between conditions of moisture and the rate of growth. Ann. of Roy. Bot. Gard., Peradeniya **2:** 211–267. 1904.

(20) MAINS, E. B. The relation of some rusts to the physiology of their hosts. Amer. Jour. Bot. **4:** 179–220. 1917.

(21) MELHUS, I. E. Germination and infection with the fungus of the late blight of potato. Wisconsin Agr. Expt. Sta. Research Bul. **37:** 1–64. 1915.

(22) PEDERSON, R. Haben Temperaturschwankungen als solche einen ungünstigen Einfluss auf das Wachsthum? Arb. Bot. Inst. Würzburg **1:** 563–583. 1874.

(23) PRICE, H. L. The application of meterological data in the study of physiological constants. Ann. Rpt. Virginia Agr. Expt. Sta. **1909/10:** 206–212. 1911.

(24) RAVAZ, L. AND VERGE, G. Influence de la température sur la Germination des conidies du mildiou. Prog. Agr. et Vit. **57:** 170–177. 1912.

(25) RAVN, F. KOLPIN Nogle Helminthosporium-Arter og de af dem fremkaldte Sygdomme hos Byg og Havre. Bot. Tidskr. **23:** 101–322. 1900.

(26) SACHS, J. Textbook of botany. Translated by Alfred W. Bennett assisted by W. T. Thistleton-Dyer. Oxford, 1875.

(27) SHAPOVALOV, MICHAEL Effect of temperature on germination and growth of the common potato-scab organism. Jour. Agr. Research **4:** 129–133. 1915.

(28) SHIBATA, K. Beiträge zur Wachstumsgeschichte der Bambusgewächse. Jour. of Sci. Imp. Univ., Tokyo **13:** 329–496. 1900.

(29) TISDALE, W. H. Relation of temperature to the growth and infecting power of Fusarium lini. Phytopathology **7:** 356–360. 1917.

(30) TRUE, R. H. On the influence of sudden changes of turgor and of temperature. Ann. Bot. **9:** 365–402. 1895.

(31) WIESNER, JULIUS Untersuchungen über den Einfluss der Temperatur auf die Entwicklung des Penicillium glaucum. Sitzber. Akad. Wiss. (Vienna) Math. Naturw. Kl. **68:** 5–16. 1874.